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Influence of a litter feeding earthworm, *Lumbricus rubellus*, on soil processes in a simulated coniferous forest floor

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1. Introduction

The beneficial influence of earthworms on both physical and chemical properties of soil has been well documented in numerous studies (see review by Lee, 1985). Partly for this reason, there has been increasing interest in introducing earthworms into areas or ecosystems without native populations. In many cases these introductions have been successful: populations have become established, and positive effects e.g. on plant growth, have been observed (Barley & Kleinig, 1964; van Rhee, 1969; Stockdill, 1982; Hoogerkamp et al., 1983).

Because boreal coniferous forests are unfavourable habitats for earthworms, such forests are inhabited by only low densities of a few species. Huhta (1979) and Huhta & Kulmala (1987) have shown that coniferous forest soil could be rendered more favourable for earthworms by liming and/or adding leaf litter. Thus, it might be possible for litter feeding species like *Lumbricus rubellus* to reproduce and/or disperse from surrounding areas, provided there are deciduous trees to produce palatable leaf litter.

Haimi & Huhta (1990) have shown that, when feeding on birch leaf litter, *L. rubellus* can increase pH and enhance the mineralization of nutrients (especially nitrogen) in raw humus. This finding led to a study of the performance of *L. rubellus* in a more complex system in which mineral soil and diverse fauna were included. The aim of the present study was to determine the contribution of *L. rubellus* to the soil processes in coniferous forest floor.

2. Material and methods

2.1. Materials

The mineral soil used in this experiment was taken from a sand-pit near Jyväskylä, Central Finland. The soil was sieved through a 4 mm sieve and washed to remove organic material. After washing, the pH was 5.0 and the organic matter content was 0.46% (mass). Humus from an adjacent moist coniferous forest was sieved through a 20 mm mesh and used while still fresh. The pH of this humus was 4.1, the organic matter content was 71.8% and the water content was about 75%. Birch leaf litter (*Betula pendula* Roth) was collected under one tree a few weeks after leaf-fall, and stored at $-28\,^{\circ}C$ until used. Adult earthworms (*L. rubellus* Hoffmeister) were sampled by hand.

2.2. Experimental design

The experiment was carried out in plastic vessels (bottom area $0.085\ m^2$) with airtight lids (see Haimi & Huhta, 1990). Three kilograms of mineral soil (dry mass; about 6 cm layer) was spread on the bottom of each container, covered with a cotton net (3 mm mesh), and watered with 500 ml of distilled

water. Then 500 g of humus (126.1 g dry mass) was added and covered with a similar net. Finally, 13 g of (d.m.) birch leaf litter was spread on the upper net. At week 55, before the second "winter" (see explanation below), 6 g of the same litter was added to each vessel. A total of 16 identical "habitats" were constructed, and ten adult specimens of *L. rubellus* were introduced into eight of the replicates (mean fresh mass with gut contents was 2.90 ± 0.21 g). At week 83, four adult specimens of *L. rubellus* were added to the remaining vessels containing worms (mean f.m. was 3.44 ± 0.38 g).

The vessels were incubated at a constant temperature of 16 °C, except during simulated winter conditions. The first "winter" was between weeks 6 and 18 when the temperature was lowered stepwise to +2 °C during weeks 6–8 and raised again during weeks 16–18. The second "winter" began at week 60 and ended at week 72 (the temperature was lowered during weeks 60–63, and raised during weeks 70–72).

For analyses of nutrient contents in the leachates, the vessels were irrigated 11 times with distilled water. Half of the replicates (4 + 4) were destructively sampled at week 45, and the rest at week 93.

The moisture of the substrates remained rather constant throughout the experiment. Nor were there differences between treatments in the amounts of water leached through the soil or in the water-holding capacity.

2.3. Analyses

As a rule CO_2-evolution was measured weekly with an infra-red carbon analyzer (URAS 7N). The air current (flow rate about $15 \, l \, h^{-1}$) was conducted from a compressor through the vessels to the analyzer (for details, see Haimi & Huhta, 1990).

pH, NH_4-N, NO_3-N, total N (the latter including soluble organic, inorganic and particulate nitrogen), PO_4-P and total C were analysed from the leaching waters; N and P were determined photometrically (see HAIMI & HUHTA, 1990). Samples for NH_4-N and PO_4-P analyses were filtered through an ultrapure filter. Other analyses, with the exception of NO_3-N and total N, were made on all replicates at every irrigation. NO_3-N and total N were analysed in every second replicate before the first destructive sampling, and later on (from the 7th irrigation onwards) in all replicates (NO_3-N was not measured at the 1st, 2nd and 5th irrigations).

At the destructive samplings, the humus layer and the upper and lower layers (3 cm each) of mineral soil were studied separately. Mass loss, organic matter content, pH (from water solution), KCl-extractable (2M) NH_4-N, NO_3-N, total N and PO_4-P were analysed, and the numbers of animals were counted. Analyses of the nitrogen content of dry matter were made with a Carlo Erba 1106 Elemental Analyzer at week 45, and with a Kjeldahl digestion system at week 93. At week 45 worm surface casts were also analysed.

From separate subsamples, enchytraeids and hatchlings of earthworms were extracted by the wet funnel method (O'CONNOR, 1962), nematodes with modified wet funnels (SOHLENIUS, 1979), and microarthropods (Collembola and Acari) with a high gradient cylinder extractor (MACFADYEN, 1961).

Potential rate of denitrification was determined in a parallel microcosm experiment that was constructed similarly. The method was based on the inhibition of nitrous oxide (N_2O) to gaseous nitrogen by acetylene gas (KASPAR & TIEDJE, 1980; LUMME & LAIHO, 1989). Four vessels contained normal (70% in humus) moisture content, and two others were wet (80%). Every second vessel was inoculated with *L. rubellus*. Samples (humus: 2–3 g d.m. and mineral soil: 26–40 g d.m.) were taken 5, 7 and 8 weeks after establishment of the experiment and transferred to sterilized bottles (volume about 130 ml). Water was added to about 200% of the water retention capacity of the soil. The bottles were closed with air-tight rubber stoppers, and a vacuum was created inside. To replace the air, nitrogen gas was injected through a stopper followed by 5–10% (by volume) acetylene gas. The bottles were incubated at about 16 °C. After one week, gas samples were taken from the bottles, and N_2O was measured using a gas chromatograph with an EC-detector (chromatographic separation in a metal column packed with Porapack Q).

3. Results

3.1. Animal populations

The numbers of enchytraeids, Collembola and mites increased during the first 45 weeks, but decreased by the second destructive sampling at week 93 (table 1). The populations were more abundant in the control vessels than in the presence of *L. rubellus*. The initial

Table 1. Numbers of animals other than earthworms per vessel (mean and S.D.).

	At start	Week 45		Week 93	
		Control	L. rubellus	Control	L. rubellus
Enchytraeidae	82 (57)	5626 (1460)*	2913 (857)	31 (48)	4 (7)
Nematoda	13000 (9800)	10154 (1137)**	4226 (1140)	8062 (10534)	17235 (17180)
Collembola	318 (164)	2716 (1418)*	513 (302)	912 (675)	318 (154)
Mesostigmata	186 (77)	575 (121)**	199 (59)	12 (13)	84 (72)
Other mites	2517 (247)	3326 (1887)	1653 (446)	3016 (1108)	2235 (635)

Note: Significant differences between controls and vessels with *L. rubellus* are indicated with asterisks (Student's t-test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n = 4).

(added) biomass of enchytraeids [*Cognettia sphagnetorum* (VEJD.)] was only ca. 10 mg (fresh) per vessel. At week 45 there was ca. 1.6 g per vessel in the control set, and 0.8 g in the *L. rubellus* set (biomass determination according to HUHTA et al. (1979) for *C. sphagnetorum*).

There was considerable mortality of *L. rubellus* during the experiment (table 2). Some cocoons or small hatchlings of another species, *D. octaedra*, were introduced into both treatments with the humus. These grew and reproduced so well that at week 45 the earthworm biomass was the same in both the *L. rubellus* set and the control (table 2).

Table 2. Numbers and biomasses (g fresh mass, gut contents included) of earthworms, and cocoons produced per vessel (mean and S.D.).

	At start	Week 45	Week 93
Numbers:			
Control	--	4.00 (0.82)	2.80 (4.40)
L. rubellus	10 (+4[1])	3.00 (0.82)[2]	7.55 (1.90)[3]
Biomass:			
Control	--	0.47 (0.17)	0.07 (0.08)
L. rubellus	2.90 (0.21) +3.44 (0.38)[1]	0.48 (0.20)	1.24 (0.32)
Cocoons:			
Control	n.d.	39 (23)	8 (6)
L. rubellus	n.d.	21 (22)	6 (13)

[1] earthworms added at Week 83
[2] 0.3 of *L. rubellus*
[3] 6.8 of *L. rubellus*
Note: All earthworms in controls were *D. octaedra*.

3.2. Carbon losses

The CO_2-evolution in the vessels with *L. rubellus* was sometimes higher and sometimes lower than in the controls (Fig. 1). After 45 weeks, 13.0 g of carbon had been respired from the control vessels, and 12.0 g from those with *L. rubellus*. After 93 weeks, the carbon losses via respiration were 16.8 g in the controls and 16.3 g in the presence of *L. rubellus*. Cumulative CO_2-production was calculated based on the assumption that the change between measurements was linear.
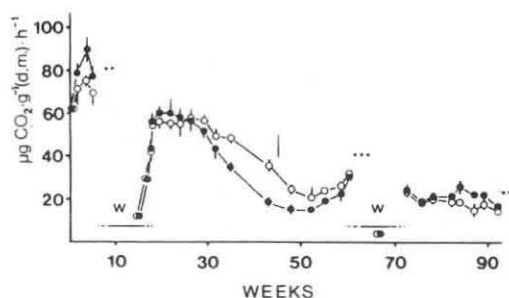
Fig. 1. Instantaneous evolution of CO_2 (mean $\pm$ SE). o——o = Control; •——• = with *L. rubellus*. W = winter. Significant differences for periods: before first winter, first winter — week 45, week 48 — second winter and after second winter are indicated with asterisks (multivariate analysis of variance for repeated measurements: ** $P < 0.01$; *** $P < 0.001$); n = 8 before Week 45 and 4 after that).

Carbon contents in the leachates were measured only until week 50. The cumulative leaching of C averaged 46.3 mg C in the controls, and 37.9 mg C in the vessels with *L. rubellus*.

L. rubellus effectively consumed litter from the soil surface. In the presence of *L. rubellus*, the organic matter content of the humus decreased, and that of mineral soil increased. The total mass loss was higher in the controls than in the vessels containing *L. rubellus* (table 3).

Table 3. Amounts of remaining litter, contents of organic matter (%), and total organic matter (g) in the systems.

	At start	Week 45		Week 93	
		Control	*L. rubellus*	Control	*L. rubellus*
Litter (g)	13.0 +6.0	4.39 (0.49)***	1.10 (0.42)	7.97 (1.40)***	1.49 (0.88)
Organic matter, %:					
Litter	94.4	93.6	93.7	93.6	93.7
Humus	71.0 (4.1)	60.2 (3.4)	57.7 (1.7)	54.4 (1.8)**	50.3 (1.4)
Upper mineral	0.46 (0.01)	0.84 (0.04)***	1.27 (0.11)	0.80 (0.14)*	1.13 (0.12)
Lower mineral	0.46 (0.01)	0.49 (0.01)	0.51 (0.06)	0.53 (0.01)	0.54 (0.03)
Castings			26.5		
Org. mat. (g)	121.3	93.8 (2.8)	96.1 (1.4)	89.66 (3.0)	92.5 (1.5)

Note: Significant differences (Student's t-test) are indicated with asterisks as in table 1. See text for further explanations.

3.3. Phosphorus and nitrogen

The leaching of $PO_4 - P$ was very low in both treatments, always less than 10 µg per vessel; and no differences were found between treatments. The amounts of $PO_4 - P$ in KCl-extracts from humus were slightly higher in the presence of *L. rubellus* (table 4).

The amounts of total N and $NO_3 - N$ in the leaching waters increased sharply during the first 50 weeks, after which they again decreased (fig. 2 A and B). The concentrations of $NH_4 - N$ in the leachates were small compared with those of $NO_3 - N$ (fig. 2 C). With few exceptions, during the first 50 weeks significantly more nitrogen was leached from the vessels containing *L. rubellus* (fig. 2).
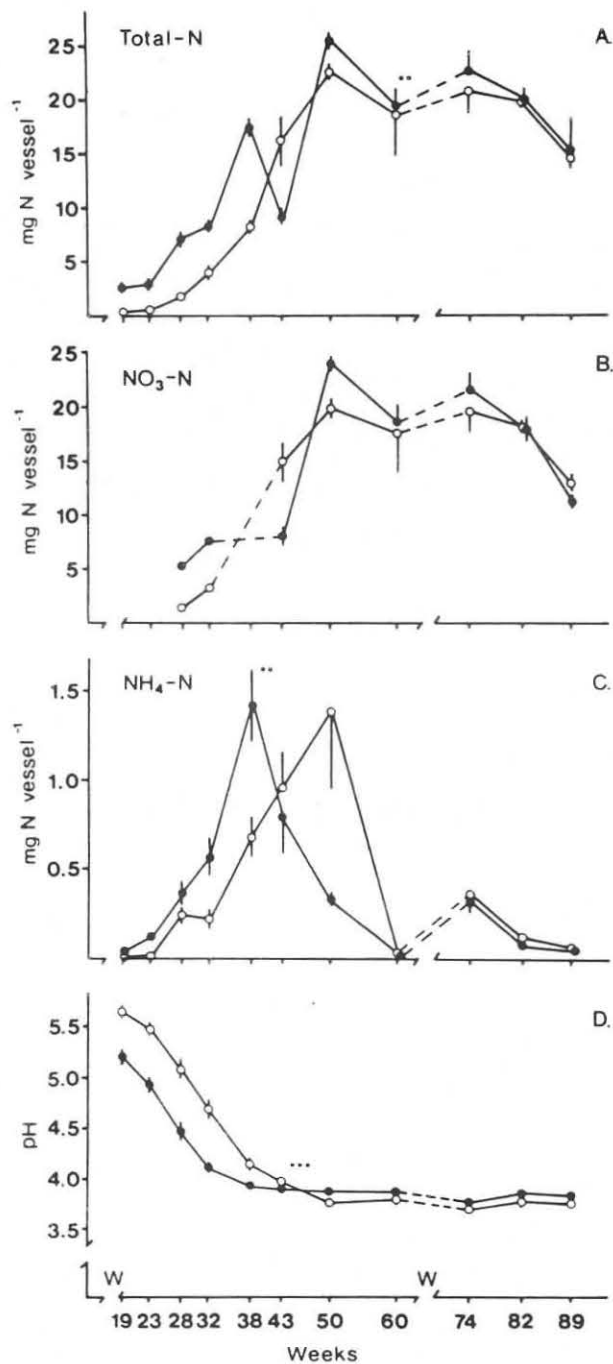
Fig. 2. pH and amounts of nitrogen in leaching waters (mean ± SE). o——o = Control; ●——●
= with *L. rubellus*. W = winter. Significant differences for certain periods (multivariate analysis of
variance for repeated measurements) as in Fig. 1.

Table 4. *p*H and amounts of KCl-extractable nutrients in humus, upper (Upperm) and lower (Lowerm) parts of mineral soil, and in casts of *L. rubellus* (µg nitrogen/phosphorus per g substrate ± S.D.).

		Initial	Week 45		Week 93	
			Control	*L. rubellus*	Control	*L. rubellus*
pH:	Humus	4.15	4.80 (0.09)***	4.17 (0.02)	4.30 (0.03)	4.30 (0.03)
	Upperm	4.95	4.39 (0.11)	4.24 (0.06)	4.22 (0.03)	4.24 (0.04)
	Lowerm	4.95	4.28 (0.12)	4.19 (0.07)	4.24 (0.03)	4.22 (0.02)
	Casts	—	—	4.32 (0.03)	—	—
TN:	Humus	354.0	756.6 (62.9)	789.1 (47.7)	546.2 (54.2)*	560.6 (35.7)
	Upperm	5.9	25.8 (2.7)**	45.0 (5.6)	22.5 (1.5)**	29.5 (2.4)
	Lowerm	5.9	25.4 (2.7)*	34.4 (4.3)	22.4 (2.2)	25.3 (1.8)
	Casts	—	—	493.1 (10.4)	—	—
NO_3^-:	Humus	0.7	256.4 (60.4)**	483.3 (54.1)	393.6 (27.1)	393.5 (78.6)
	Upperm	0.2	15.2 (3.4)***	35.3 (2.3)	17.6 (2.6)*	23.2 (3.6)
	Lowerm	0.2	15.9 (3.8)**	26.8 (3.7)	17.6 (2.5)	20.0 (2.4)
	Casts	—	—	331.1 (20.8)	—	—
NH_4^+:	Humus	52.2	316.0 (36.4)***	97.5 (9.4)	24.3 (3.5)**	36.5 (6.1)
	Upperm	1.5	5.0 (0.8)*	3.2 (0.6)	¹	¹
	Lowerm	1.5	4.1 (0.1)*	2.3 (0.7)	¹	¹
	Casts	—	—	39.3 (1.9)	—	—
PO_4^{3-}:	Humus	50.6	30.6 (3.8)	35.5 (2.1)	17.9 (3.2)	20.0 (2.3)
	Upperm	0.1	0.9 (0.3)*	1.7 (0.4)	¹	¹
	Lowerm	0.1	0.06 (0.01)	0.05 (0.02)	¹	¹
	Casts	—	—	34.7 (0.3)	—	—

¹ not measurable concentration

Note: TN = total nitrogen. Significant differences as in table 1. n = 4 except in initial materials.

After 45 weeks incubation there was more KCl-extractable total N and $NO_3 - N$, but less $NH_4 - N$ in the vessels with *L. rubellus* (table 4). After 93 weeks the positive influence of *L. rubellus* was evident for all forms of nitrogen (table 4). In the mineral soil there were only small amounts of extractable nitrogen, and no marked differences between the upper and lower layers (table 4).

The casts of *L. rubellus* collected at week 45 contained less nitrogen, but had about the same amount of phosphorus as the surrounding humus. The *p*H of the casts was higher than that of the humus (table 4).

Owing to earthworm mortality, the nitrogen pool was larger in the *L. rubellus* replicates than in the controls. It was estimated (using the nitrogen content of 8.7% obtained by HAIMI & HUHTA, 1990) that the additional amount of N in the vessels with *L. rubellus* averaged 27.4 mg at week 45 and 59.3 mg at week 93.

Hardly any denitrification was found to take place in the soil, not even in the vessels that were kept wet. A measurable amount of N_2O was found only in one humus sample (a vessel without *L. rubellus*).

The total (dry matter) nitrogen content of litter clearly increased during the experiment, and even more so in the controls. The nitrogen content of humus increased at first, but by week 93 had decreased to the initial level (table 5).

3.4. *p*H

The pH of the leaching water decreased in both treatments during the first 40 – 50 weeks, but was significantly lower in the presence of *L. rubellus* (fig. 2 D).

At week 45, the pH of humus had increased in the controls but not in the presence of *L. rubellus*. The *p*H of mineral soil decreased in both treatments. At weeks 93, there were no differences between vessels with and without *L. rubellus* or between the different soil layers (table 4).

Table 5. Contents of nitrogen (% of d.m.) in litter and humus. n = 2 if S.D. not presented, otherwise n = 4.

| | Initial | Week 45 | | Week 93 | |
		Control	L. rubellus	Control	L. rubellus
Litter	0.82	1.77 (0.07)**	1.54 (0.08)	1.8	1.2
Humus	0.90	1.04 (0.17)	1.07 (0.16)	0.91 (0.01)*	0.80 (0.06)

Note: Significant differences between controls and vessels with L. rubellus as in table 1.

4. Discussion

Compared with the previous experiment where only organic material was used (HAIMI & HUHTA, 1990), addition of a mineral soil layer below the humus horizon affected many soil chemical variables. First, the pH of the leachates decreased over time, and was **lower** in the presence of L. rubellus than in the control soil. Second, most of the ammonium nitrogen was rapidly nitrified, also in the humus. This phenomenon obviously caused the reduction in pH (see HAIMI & HUHTA, 1990). Finally, either leachates or KCl-extracts from the mineral soil contained virtually no $PO_4 - P$. In addition, the amounts of nitrogen leached in this experiment were much greater than those leached from organic matter only (HAIMI & HUHTA, 1990).

L. rubellus effectively removed litter from the soil surface, increased the amounts of all forms of nitrogen in the leachates, and decreased the pH of leachates during the first half of the experiment. Later on, their influence levelled out. The introduction of new worms was reflected only in the evolution of CO_2, not in pH values or nutrient concentrations of the leachates. The influence of L. rubellus on the soil properties was less obvious than reported previously (HAIMI & HUHTA, 1990). There may be several reasons for this difference. For example, the survival rate of L. rubellus was even lower than in the previous experiment with organic matter only (HAIMI & HUHTA, 1990). Obviously, the worms did not manage to reproduce before the first winter, and the adults died during the first winter and the following summer (see also HAIMI & HUHTA, 1990). On the other hand, it should be noted that in this experiment the controls had a very diverse fauna including also earthworm D. octaedra. This species thrived, and without doubt partly masked the effects of L. rubellus (cf. HAIMI & HUHTA, 1990).

The dense population of the enchytraeid C. sphagnetorum at the first destructive sampling (week 45) must be emphasized. At that time the numbers of enchytraeids were high even compared to natural soils (HUHTA et al., 1986), and their biomass was greater than that of earthworms. Obviously, at these densities they influence soil processes. For instance, STANDEN (1978) showed that C. sphagnetorum increases the rate of mass loss of Calluna and Eriophorum litter. In addition, WILLIAMS & GRIFFITHS (1989) found that enchytraeids enhance mineralization and leaching of N, P and many base cations from spruce litter. The fact that the C. sphagnetorum population was denser in the controls than in the L. rubellus replicates probably influenced the results for the variables measured more in the control conditions.

The nitrogen derived from dead biomass could, at least in the theory, explain the surplus of N in the presence of L. rubellus; but as discussed by HAIMI & HUHTA (1990), this was obviously not the case. The nitrogen liberated from dead biomass is immobolized by microbes rather than directly leached from the soil. It should also be remembered that there were decaying enchytraeids present in the vessels between weeks 45 and 93, especially in the controls.

The present experiment demonstrates the importance of *L. rubellus* in mixing litter into the soil (although it is usually regarded as a surface-dwelling species). These worms incorporate humus and casts (organic matter) into the mineral soil, although not much deeper than the upper layer of 3 cm. The mineral soil contained more extractable nitrogen and phosphorus in the presence of *L. rubellus*. SYERS *et al.* (1979) also pointed out that *L. rubellus* is important in incorporating litter N into the soil in permanent pastureland.

L. rubellus did not affect the total mass loss from the system, but did have a positive effect on CO_2-evolution during the period when active worms were present. Without a doubt when the enchytraeids were abundant they also stimulated microbial respiration (*cf.* STANDEN, 1978), and during certain periods played a greater role than *L. rubellus* did (e.g. weeks 30 — 60).

L. rubellus had a positive effect on nitrification in all soil layers; this was especially evident in the KCl-extracts. Haimi & Huhta (1990) found that hardly any nitrification took place in their experiment with organic horizon only; but PARLE (1963), SYERS *et al.* (1979), SCHEU (1987) and McCOLL *et al.* (1982) observed enhanced nitrification due to earthworms in different kinds of soil. Thus, in soils where nitrifying microbes are active, their function is obviously enhanced by earthworms.

Denitrification did not take place in our experimental forest floor, not even in a substrate that was wet. In their laboratory study, SVENSSON *et al.* (1986) found higher rates of denitrification in the casts of *L. terrestris* than in the surrounding arable soil. On the other hand, although KAPLAN & HARTENSTEIN (1977) found no evidence of nitrogen fixation or reduction of nitrate to nitrite in many species of earthworms (including *Lumbricus* sp.), SIMEK & PIZL (1989) observed that *L. rubellus* had clearly positive effect on nitrogenase activity (N_2-fixation) in the soil (brown earth). N_2-fixation is probably very low in homogenous and acid soil (see GRANHALL & LINDBERG, 1980) however, and in our experiment the nitrogen flow between air and soil was obviously negligible.

Without doubt *L. rubellus* enhances nitrogen cycling in experimental conditions, but we are far from understanding their potential role in the field. If we could affect the field populations of *L. rubellus*, these litter-feeding earthworms might have positive effects on soil processes and tree growth in coniferous forests.

5. Acknowledgements

6. References

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The earthworm *Lumbricus rubellus* was studied in the laboratory to determine its effect on decomposition and nutrient mineralization in simulated coniferous forest floor. The control systems had a diverse soil fauna including the earthworm *Dendrobaena octaedra*. Special attention was paid to the effects of the mineral soil horizon on soil processes. CO_2-evolution was monitored; and nutrients in the leaching water were measured. The systems were destructively sampled twice; numbers of animals, pH, contents of organic matter and KCl-extractable nutrients were analysed separately from organic and mineral soil horizons.

L. rubellus affected the mineralization of nitrogen positively and also enhanced nitrification. The presence of *L. rubellus* led to decreased pH in the leaching water (even more than 0.5 pH-units). Owing to earthworm mortality, the influence of worms on the soil processes studied diminished over time. Leaching of $PO_4 - P$ through mineral soil was extremely low.

Animals other than earthworms increased their numbers until the first destructive sampling, after which they decreased. The enchytraeid *Cognettia sphagnetorum* was especially abundant at the first sampling, when its biomass was even larger than that of the earthworms (enchytraeid biomass was smaller when *L. rubellus* was present than when it was absent). Enchytraeids influenced soil processes, especially CO_2-evolution. The other earthworm *D. octaedra* grew and reproduced well in both the absence and in the presence of *L. rubellus*.

Key words: Earthworms, *Lumbricus rubellus*, Nutrient cycling, Raw humus, Forest soil.

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